Beyond the ‘deep reef refuge’ hypothesis: a conceptual framework to characterize persistence at depth

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Abstract

The rapid deterioration of coral reefs worldwide has led to a growing interest in identifying areas that can offer protection against adverse conditions including coral reef communities at intermediate (~15–30 m) and mesophotic (≥ 30 m) depths. However, various concepts regarding the protective potential of deeper coral reef communities, and subsequent roles in overall reef resilience and persistence, remain poorly defined. Herein, we organize these ideas into an initial conceptual framework, and review for scleractinian corals how these ideas may be supported by the limited empirical data that is currently available. We distinguish between the concepts of “depth refuges”, “depth refugia” and “depth resilience areas”, based on the nature (i.e., avoidance versus resilience) and temporal scope of protection. Although past examples have confirmed the role of mesophotic coral ecosystems as short-term, ecological “refuges”, there is thus far little support that they comprise long-term “refugia.” In contrast, the concept of “deep resilience areas,” reefs that persist long-term through disturbance by resistance and recovery, remains largely unexplored. In terms of the functional roles of such protected areas in the overall coral reef ecosystem, we distinguish between the concepts of “reseeding” and “local persistence”. The potential to actively reseed shallow reefs may be ecologically important, but only for a small proportion of shared biodiversity, whereas the potential to promote persistence of local biodiversity may apply across a broad range of coral reef species. Although empirical evidence remains very limited, we hope that the incipient conceptual delineations presented here provide a constructive reference for further discussion and research into the ecological importance of deep reef communities.

Keywords: Mesophotic coral ecosystems, depth, coral reefs, refuges, refugia

1. Introduction

Coral reefs are under threat due to the increasing impacts from local and global anthropogenic stressors, which have already resulted in an unprecedented decline in their health and abundance (Hughes et al. 2003; Pandolfi et al. 2003; Hoegh-Guldberg et al. 2007; Mumby et al. 2007). Due to the rapid warming of the oceans, we have seen an increase in the frequency and magnitude of both storm and thermal bleaching events, which has led to high rates of coral mortality, effectively eliminating a substantial proportion of living coral populations on reefs worldwide (De’ath et al. 2012; Hughes et al. 2017a, 2017b). Consequently, there has been increasing interest in identifying areas that can offer a temporary or long-term escape from such disturbances (Glynn 1996; Riegl and Piller 2003; Karnauskas and Cohen 2012; van Hooidonk et al. 2013; Cacciapaglia and van Woesik 2015; Smith et al. 2017b), or alternatively, that can persist due to higher resilience (Guest et al. in revision). Such areas can range from geographic regions (e.g., cooler temperatures associated with higher latitude) and localities (e.g., with favorable oceanographic conditions or wind-exposure protection), to distinct habitats within a reef system (Glynn 1996; Keppel and Kavousi 2015). Identification of such areas is crucial in marine protected area planning, to safeguard coral reefs from other stressors and promote the potential of such areas to act as a source of propagules to recolonize affected areas (Ridgway and Hoegh-Guldberg 2002; McCook et al. 2009; Guest et al. in revision).

Deeper zones of coral reefs represent a major habitat type that may be protected from, or less impacted by, major disturbances such as temperature anomalies and storm events (reviewed in Bongaerts et al. 2010). Given that these deeper zones often occur directly adjacent to shallow reefs, they may be particularly important for maintaining biodiversity within a particular location. One of the first mentions in the literature related to the concept of providing an escape to disturbances was by Glynn (1996), who proposed that coral communities at “moderate depth” may be protected from rapid ocean warming. A specific example was that coral communities below 10 m depth in certain locations of the Pacific Ocean experienced lower bleaching and mortality rates than shallower communities during the 1997–1998 El Niño Southern Oscillation (ENSO) event (Feingold 2001; Glynn et al. 2001). This concept logically extends to even greater depths and other depth-dependent

disturbances, and in that capacity, became adopted in association with deep or mesophotic coral ecosystems (MCEs; 30–150 m). Hughes and Tanner (2000) mentioned the potential of deep coral populations in Jamaica escaping the effects of hurricanes (and the mass *Diadema antillarum* die-off), and proposed their subsequent potential to serve as a larval source to aid in shallow reef recovery. Lesser et al. (2009) discussed a further broadening of this concept to include fish communities, and argued the critical importance of understanding the source-sink dynamics of shallow and mesophotic reefs for management. Unifying these various ideas, the concept of MCEs as a reproductive refuge became known as the ‘deep reef refuge/refugia’ hypothesis (DRRH; Bongaerts et al. 2010).

Characterizing the role of MCEs in overall reef resilience has become a major theme in MCE research (particularly when considering upper mesophotic depths of 30–60 m), and different aspects of the refuge/refugia capacity have been referred to in the majority of mesophotic-related publications over the past 10 years (www.mesophotic.org). Much research has focused on testing specific, isolated assumptions underlying this concept; however, the inherent complexity of the topic and its poor conceptual delineation have resulted in a certain degree of miscommunication (e.g., in supporting or disproving the DRRH). For example, the DRRH can be considered with regards to individual episodic disturbances on an ecological timeframe (e.g., Bongaerts et al. 2017), or long-term protection against changing climatic conditions (e.g., Smith et al. 2016a, 2017). Furthermore, the impacts of disturbances over depth are often not straightforward and can vary spatially and temporally (Harmelin-Vivien and Laboute 1986; Smith et al. 2016a), and strongly depend on the taxonomic group (e.g., sessile or mobile taxa) and specific taxon considered. Similarly, the subsequent functional role of safeguarded biota, can be evaluated in terms of reseeded habitats (Bongaerts et al. 2010; van Oppen et al. 2011; Serrano et al. 2014, 2016) to ensuring local species persistence (Bongaerts et al. 2013a; Muir et al. 2015).

To provide a reference for further discussion, we organized the various ideas associated with the DRRH into an initial conceptual framework. We separately assessed: (a) the potential of communities at greater depths (and in particular those at mesophotic depths) to escape or persist through disturbances, and (b) their potential contribution to the resilience and persistence of the broader coral reef ecosystem (i.e., including shallower depths). For the purposes of this discussion, we focused specifically on scleractinian corals as the framework builders of coral reefs, while acknowledging that some of the discussed concepts are not

93 directly transferable to mobile taxa such as reef fishes. We provided an overview of the
94 empirical work on: (1) the impact of reef disturbances over a depth gradient as it relates to
95 mesophotic corals being able to avoid or persist through disturbances, and (2) species overlap
96 and connectivity across a depth gradient in the context of how areas of refuge or persistence
97 may contribute to overall reef resilience. Recognizing that the extent of empirical data
98 surrounding the DRRH remains very limited, this conceptual framework will hopefully be
99 developed further and aid in identifying future studies.

Box 1. Definitions of depth-defined areas protected from disturbance(s)

Depth refuge – a depth range that provides **short-term** buffering or shelter (i.e., avoidance) for (one or multiple) species or a biological community against a particular disturbance episode.

Depth refugium – a depth range that provides **long-term** buffering or shelter (i.e., avoidance) for (one or multiple) species or a biological community against a particular or multiple disturbances type(s).

Depth resilience areas – a depth range that harbors (one or multiple) species or a biological community that is/are resilient (due to resistance or rapid recovery, not avoidance) over the **long-term** to a particular or multiple disturbance type(s).

Functional roles of depth-defined areas protected from disturbance(s):

Reseeding – the substantial provision of viable propagules by safeguarded populations of (one or multiple) species at depth, aiding in the active recovery of disturbance-impacted shallower populations.

Local persistence – the safeguarding of (one or multiple) species, effectively negating local/regional species extinction, but with limited to no potential to aid in the recovery of shallow-water populations. The number of safeguarded individuals may be minimal and/or connectivity with a disturbed habitat at an adjacent depth may be limited or non-existent.

2. Impact of reef disturbances over a depth gradient

Depth can attenuate the physical magnitude of some potential stressors and disturbances that are increasingly affecting shallow coral reefs (Bongaerts et al. 2010). However, the ultimate impact of disturbances on an ecosystem represents an interplay between the physical magnitude of such stressors and the nature of the impacted organisms (in this case the coral holobiont). For example, while physical impacts may be dampened, adaptation or long-term acclimation to milder environmental conditions at depth may result in increased susceptibility (Smith et al. 2016a). Thus, with regards to the species-specific refuge potential, both the variation of the physical magnitude of a disturbance with depth and the organism's susceptibility need to be considered. The impact of disturbances with depth was reviewed in Bongaerts et al. (2010), therefore, we provide only an updated account of the two identified primary stressors: thermal bleaching and storm events. See Smith et al. (2018) for a discussion of disturbances specifically affecting mesophotic depths.

2.1 Thermal bleaching

Thermal stress and coral bleaching (i.e., the breakdown of the coral-dinoflagellate endosymbiosis; Glynn and D'Croz 1990) can be triggered by extended periods of increased temperature (of even one degree Celsius above the mean warmest temperatures). Seawater temperatures often decline gradually with depth, and this relationship is the main reason that coral communities at intermediate depths (~15–30 m) have been looked to as potential havens for species under stress (Glynn 1996). Decreasing intensity of photosynthetically active radiation and ultraviolet light with depth bolsters the effect of declining temperature because light is a co-factor with temperature in causing bleaching (Warner et al. 1999; Muir et al. 2017).

Temperature decreases with depth can vary strongly across regions and locations, and usually depend on the depth of the upper mixed layer (i.e., the zone from the ocean surface to the first thermocline, homogenized by wind and water currents; Mann and Lazier 1996). During the warmer summer months, the boundary of the upper mixed layer roughly corresponds to the beginning of the mesophotic zone (~30–60 m) in most regions where coral reefs occur (de Boyer-Montégut et al. 2004). This includes the Caribbean Sea, Red Sea, Persian Gulf, and as you move away from the equator in the Pacific and Indian Oceans. In fact, the upper mixed

layer often becomes shallower in the warmest parts of the year (de Boyer-Montégut et al. 2004), and can result in cooler temperatures on MCEs relative to shallow reefs (Smith et al. 2016a). In other regions, such as equatorial western ocean basins, the upper mixed layer can be very deep during the warmest parts of the year, and encompass the lower mesophotic zone (> 60 m; Colin 2016). On the other end of the spectrum, areas with strong seasonal or continuous upwelling, may have sufficiently low temperatures at mesophotic depths, thereby, precluding coral development (Smith et al. 2017).

Lower temperatures at depth do not necessarily convey protection against coral bleaching as the coral's response depends on its previous thermal exposure(s) (Smith et al. 2016a). Since the coral-algal holobiont tends to acclimate to long-term thermal conditions (Coles 1976; McClanahan et al. 2007), bleaching thresholds may be lower at depth. Thus, despite cooler temperatures, coral communities at depth may only be protected when cumulative temperature exposure does not exceed the long-term conditions of that depth range. The ability of deeper coral communities to escape or resist thermal anomalies can be difficult to predict spatially and can vary from event to event (i.e., sometimes they are impacted and sometimes they are not; Smith et al. 2016a). While bleaching is generally dampened over depth (Fisk and Done 1985; Wilkinson and Souter 2008), there are examples of bleaching extending into mesophotic depths (Lang et al. 1997; Bunkley-Williams et al. 1991; Smith et al. 2016a; Reed et al. 2018) including occurrences of bleaching at mesophotic depths when nearby shallower reefs are not bleached (Smith et al. 2016a).

2.2 Storm events

Storms can have major impacts on coral reefs, and while classified as a natural disturbance, the increasing magnitude of storm events has been linked to global warming (Knutson et al. 2015). Although the mechanical force of water turbulence from surface waves caused by storms decreases linearly with depth, turbulence generated by a long-period swell can reach upper mesophotic depths and may be strong enough to affect and influence broad patterns of reef development (Groves 2016; Smith et al. 2016b, 2018). Indirectly, storm-generated coral debris and landslides on steep slopes can also transfer shallow-water impacts to MCEs (Harmelin-Vivien 1994; Colin 2016). Fine sediment can also become suspended and deposited further down the slope, smothering mesophotic corals (Hubbard 1992; Bak et al. 2005).

The impact of direct and indirect storm effects can be exacerbated when the coral community is dominated by fragile coral growth forms, such as thin plating agariciid corals (Kahng et al. 2010; Smith et al. 2010; White et al. 2013). Massive corals appear to be more resistant to such damage, but if damaged, they may need a longer time period to recover due to slower growth rates (e.g., as observed in mesophotic populations of Caribbean orbicellid corals; Weinstein et al. 2016; Groves et al. 2018). Thus, the impact of a major storm event over depth can vary strongly depending on the particular storm, the local geomorphology, and the ecological community present. Although mesophotic depths are not necessarily protected against the effects of storm damage (e.g., Robbart et al. 2009; Bongaerts et al. 2013b), there are many examples of storm damage being limited to shallower depths (e.g., Highsmith et al. 1980; Woodley et al. 1981; Kobluk and Lysenko 1992; Bak et al. 2005), demonstrating the storm refuge potential of mesophotic depths (≥ 30 m).

3. Depth offering protection against disturbance(s)

Protection against disturbances at depth can occur in many shapes and forms (Smith et al. 2017). Protection can be from specific disturbance events (e.g., thermal anomalies or storms events) or a range of stressors associated with shallower waters. It can relate to extrinsic protection by avoiding disturbance altogether or to intrinsic protection through high levels of resilience (e.g. persistence through a disturbance event or rapid recovery post-disturbance). Protection can be conferred during a short-time period (i.e., days to months), repeatedly over longer time periods (i.e., years to decades), or over evolutionary timescales (i.e., thousands of years). Here, we outline that based on the scope, nature, and temporal context of protection, different scenarios of protection at depth can be categorized as *depth refuges*, *depth refugia*, or *depth resilience areas* (Figs. 1 and 2). These can then be further specified based on the bathymetry and ecological scope of protection (Fig. 2). Although we adopt the terms *refuges* and *refugia* (sensu Keppel et al. 2012), we acknowledge that these terms are often used interchangeably in the coral reef literature (Kavousi and Keppel 2018), and occur as doublets in the English language (sharing the same etymological root).

3.1 *Depth refuge*: short-term avoidance of a disturbance

Refuges (i.e., plural of *refuge*) have been broadly defined as areas that provide short-term “spatial and/or temporal protection from disturbances or advantages in biotic interactions”

(sensu Keppel et al. 2012). We define a *depth refuge* for coral reefs as a depth range that provides short-term buffering or shelter (i.e., avoidance) for (one or multiple) species or a biological community against a particular disturbance event (Fig. 1). A depth refuge can be relatively shallow (e.g., 10–15 m), or include mesophotic depths (> 30 m). While depth refuge is inclusive of mesophotic depths, we specifically refer to a *mesophotic refuge* when the depth refuge considered is at depths below 30 m. Conversely, an *inverse depth refuge* would refer to a refuge at depths shallower than the impacted depth range, for example, in the case of a density-driven inversion in temperatures over depth (Neal et al. 2014). The depth ranges of refuges are rarely discrete, and more likely represent arbitrary delineations over an impact gradient. In terms of ecological scope, a refuge can be restricted to the protection of an individual species, multiple species, or apply to the broader ecological community within the affected depth range (although the level of protection likely varies among species). It is important to note that in this definition, the term refuge does not necessarily imply a functional role (e.g., the ability to act as a source of recruitment).

Examples of *thermal depth refuges* at shallow depths have been reported particularly in the Eastern Tropical Pacific Ocean (reviewed in Smith et al. 2017) and Indo-Pacific Ocean. In Ecuador (Galápagos Islands and mainland coast) and Panama, coral communities at depths >10 m suffered much lower bleaching and mortality rates than shallower coral communities (Feingold 2001; Glynn et al. 2001). Similarly, during the ENSO-related thermal disturbance in 2015 in the Gulf of Chiriquí (Panama), depth-generalist (i.e., with a broad depth distribution) scleractinian coral species were not impacted at depths > 15 m (T.B. Smith, unpubl. data). This included *Millepora intricata*, a species that was extirpated from shallow-water habitats during the 1997-1998 ENSO event, followed by recovery, for it to be extirpated again in the shallow during the 2005 event (Smith et al. 2014). In the Indo-Pacific, a thermal depth refuge was observed at very shallow depths (6–8 m) for *Acropora* communities in Indonesia (Bridge et al. 2013), and at shallow/intermediate-depths (10–27 m) for a large proportion of the scleractinian coral community in the Maldives (Muir et al. in 2017). Similarly, *storm depth refuges* can occur at relatively shallow depths. For example, Hurricane Allen in Jamaica mostly had an impact at depths <15 m, leaving deeper areas relatively unaffected (Woodley et al. 1981).

Although the concept of decreasing bleaching impact over depth is relatively well known and described (Fisk and Done 1985; Hoegh-Guldberg and Salvat 1995; Wilkinson and Souter

2008), specific examples of *mesophotic thermal refuges* remain largely anecdotal. Smith et al. (2016a) described a thermal refuge at mesophotic depths in the U.S. Virgin Islands, where upper mesophotic coral communities escaped thermal stress during a shallow-water bleaching event. Another example represents the species-specific mesophotic thermal refuge described for *Seriatopora hystrix* in Okinawa, which was reported to be locally extinct on shallow reefs after the 1998 and 2001 bleaching events (Sinniger et al. 2013, 2017). In terms of *mesophotic storm refuges*, there are a few studies from the Atlantic and Indo-Pacific Oceans documenting MCEs as protected from storms (e.g., Highsmith et al. 1980; Harmelin-Vivien 1994; Robbart et al. 2009). Particular with mesophotic storm refuges, protection can be associated with strongly localized conditions (e.g., slope angle, sediment transport, exposure side, and community type), rather than applying more generally to mesophotic habitats in the region, highlighting the case-specific nature of such protection.

3.2 *Depth refugium: long-term avoidance of disturbances*

Refugia (i.e., plural of *refugium*) have been broadly defined as “habitats that components of biodiversity retreat to, persist in and can potentially expand from under changing environmental conditions” (sensu Keppel et al. 2012). We define a *depth refugium* for coral reefs as a depth range that provides long-term buffering or sheltering (i.e., avoidance) for (one or multiple) species or a biological community against multiple disturbances (Fig. 1). A depth refugium relates to long-term avoidance, and in terms of scope can range from being specific to a particular disturbance (e.g., thermal depth refugium) to all possible disturbances affecting an adjacent depth range (e.g., overall depth refugium). Similarly, as with a refuge, we can either have a depth refugium referring to any specific depth range (shallow or deep), or more specifically a *mesophotic refugium*, and the ecological scope can range from individual species to the broader ecological community. As with refuge, our definition of refugium does not require a demonstrated functional role with regards to the ability to act as a source of recruitment.

Examples of *thermal depth refugia* are difficult to demonstrate because observations need to be made over multiple thermal disturbances. Modern coral reefs have only recently entered a period where thermal stress events are occurring more regularly (> once every 10 years). However, a thermal depth refugium has been suggested for the coral fauna of the Gulf of Chiriquí in the Panamanian Pacific (Glynn 1996; Smith et al. 2014, 2017), which has been

under ecological investigation since the 1970s and experiences periodic ENSO thermal anomalies (Glynn et al. 2017). Such longitudinal studies encompassing multiple disturbances are missing almost entirely for mesophotic depths, largely due to the associated logistical constraints. An exception is the nine-year study of a MCE in the U.S. Virgin Islands, which revealed that the MCE did not represent a *mesophotic thermal refugium* (Smith et al. 2016a). Although the mesophotic habitat demonstrated characteristics that could support a depth refuge, such as cooling with depth, coral bleaching thresholds also declined with depth (i.e., susceptibility increased). The system demonstrated all possible responses relative to shallow habitats, including a depth refuge (in 2010), a non-depth refuge (2005), and an inverted depth refuge, when deeper corals bleached and shallow corals did not (2012) (Smith et al. 2016a).

In contrast, examples of *storm depth refugia* may be more identifiable, as storms have been shaping coral ecosystems for millennia. However, observations of storm damage over large depth ranges still relate mostly to specific disturbances (i.e., storm depth refuges), rather than evaluation of the same area over longer time frames. Although, in the Cay Sal region of the Bahamas, shallow environments have been heavily storm-impacted, with MCEs described as better developed (Goldberg 1983), presumably through long-term avoidance. Additionally, there may be reef systems (e.g., Bermuda: Smith et al. 2013) where both shallow and mesophotic reefs are largely protected from storms, but through intrinsic protection at shallow depths (e.g., shallow communities resisting impacts due to strong long-term selection for storm-resilient, massive and encrusting coral genera) and extrinsic protection at mesophotic depths (i.e., deep enough to escape the physical impacts). Deeper reef areas that are buffered from storm impacts in the tropical storm belts may be particularly important in supporting depth refugia in the future. In the Caribbean, the interplay between storm disturbance and loss of resilience (i.e., that would allow for recovery between storms) has been posited as a major cause of coral decline (Hughes 1994; Rogers and Miller 2006). Overall, it should be noted that with multiple long-term stressors in play, such as continued increases in ocean temperature, the magnitude of storms, and acidification (Keppel and Kavousi 2015; Kavousi and Keppel 2018), an overall depth refugium role for MCEs would probably be unlikely.

3.3 *Depth resilience area: long-term resilience against disturbances*

Protection against disturbances can come from a variety of mechanisms, but is not limited to avoidance (i.e., extrinsic protection), such as in short-term refuges and long-term refugia. Coral persistence through time can also arise through resilience of the biological community (i.e., intrinsic protection), and can lead to similar trajectories of persistence as long-term avoidance (Fig. 1). However, the potential for increased resilience at depth has been rarely considered. Resilience of an ecological system to disturbance is classically defined as the combined contribution of resistance or recovery, so as to maintain essentially the same function, structure, identity, and feedbacks (Holling 1973). With regards to protection at depth, we define a *depth resilience area* as a depth range that harbors (one or multiple) species or a biological community that is resilient (due to resistance or rapid recovery, not avoidance) over the long-term to multiple disturbances. Thus, a depth resilience area deals with long-term persistence specific to a particular disturbance (e.g., thermal depth resilience area) or to all possible disturbances (e.g., overall depth resilience area). Similar to short-term depth refuges and long-term refugia, depth resilience areas can be further specified with regards to depth and ecological scope, and do not necessarily imply a functional role with regards to the overall ecosystem.

The role of resilience in supporting persistence at depth is hypothetical, but follows from ecological theory and empirical observations of shallow coral reef ecosystems (Gilmour et al. 2013). Resistance can evolve in populations through natural selection given specific environmental conditions (Baker et al. 2004), such as thermal variability (McClanahan et al. 2007). Conversely, populations at depth may exhibit enhanced recovery rates, thus experiencing disturbances through a decline in population abundances and other ecological attributes, but recovering sufficiently fast to maintain long-term persistence (Fig. 1). In part due to avoidance, mesophotic coral communities are considered to be less resilient with regards to storm impacts (due to fragile growth forms, greater susceptibility to sedimentation, and potentially slower growth rates; Bongaerts et al. 2010; Kahng et al. 2010; Smith et al. 2010), and there is initial evidence that the same may be true of thermal impacts (i.e., lower thermal bleaching threshold; Smith et al. 2016a). In the U.S. Virgin Islands, there appears to be a decline in resistance with depth and a failure to recover after a disturbance (Smith et al. 2016a). Whether this translates to other regions remains unclear, and highlights the critical importance of longitudinal studies at depth.

3.4 *Depth oases: a holistic view of persistence in the face of disturbance*

The potential of MCEs to escape disturbances, has led to a burst of inquiry in the last decade, and has undoubtedly progressed our understanding of avoidance as a mechanism to support persistence. However, the interplay between avoidance, resistance, and recovery at depth has not been holistically considered. The concept that some reefs will persist through (a combination of) avoidance, resistance, and/or recovery in certain geographic locations has recently been termed ‘coral reef oases’ (Guest et al. in revision). Thus, in a bathymetric context, there may similarly be *depth oases* or *mesophotic oases*, representing areas that are more persistent in a time of rapid environmental change. For example, rather than necessitating full avoidance to foster persistence (e.g., as in the overall depth refugium concept), a depth oasis may only offer occasional or partial avoidance from a particular disturbance. In combination with enhanced resistance and/or recovery (similar to a depth resilience area), this could then lead to a minimal long-term demographic impact of the disturbance. Similarly, a depth oasis may constitute both a storm depth refugium (i.e., long-term protection against storms) and a thermal depth resilience area (i.e., long-term protection against thermal impacts), resulting in long-term protection through a combination of mechanisms. Overall, a more holistic view of the mechanisms by which reefs persist in the face of increasing disturbance will be useful and provide more substantive information to inform ecology and management.

4. *Species overlap and connectivity across the depth gradient*

The strong environmental gradients imposed by depth are a major structuring force of marine ecosystems, analogous to elevation in terrestrial ecosystems (Rahbek 1995). On coral reefs, environmental variables such as wave action, incident irradiance, ultraviolet radiation, food availability, and temperature regimes can vary dramatically across depths (Dollar 1982; Vermeij and Bak 2002; Lesser et al. 2009). These variables can be strongly interactive and are reflected in the partitioning of ecological assemblages over depth (Done 1982), leading to distinct communities at opposite ends of the bathymetric range of coral reefs (Kahng et al. 2014). This structuring is notable across the taxonomic hierarchy, ranging from shifts in dominance of broad taxonomic groups (Kahng et al. 2010), depth partitioning of species within those groups (Goreau and Wells 1967; Sheppard 1982; Veron 2000), depth-associated genetic structuring of populations within a single species (Bongaerts et al. 2010, 2011;

Brazeau et al. 2013; Prada et al. 2013; Serrano et al. 2014, 2016), and finally, partitioning of the microbiome (e.g., *Symbiodinium* and prokaryotes) associated with a particular species (Bongaerts et al. 2015a; Hernandez-Agreda et al. 2016; Glasl et al. 2017). To understand the functional importance of safeguarded populations at depth, it is crucial to assess such zonation patterns and the resulting composition (at different taxonomic levels) of the community escaping a disturbance, so that the potential overlap with shallower communities affected by disturbance can be established.

4.1 Ecosystem-level: change in macrobiotic composition over depth

Photosymbiotic corals belonging to the order Scleractinia are responsible for producing the structural framework that supports highly diverse marine life. Other macrobenthic cnidarians such as sea anemones (order Actiniaria), soft corals and gorgonians (order Alcyonacea), zoanthids (order Zoantharia), corallimorphs (order Corallimorpharia), and fire corals (class Hydrozoa), as well as sponges (phylum Porifera) and macroalgae can all occupy substantial proportions, or dominate, the available substrate on coral reefs. Particularly over depth, the contribution of scleractinian corals to the benthic composition generally decreases, with sponges, octocorals, and macroalgae increasing (Liddell and Ohlhorst 1988; Lesser et al. 2009; Rivero-Calle 2010). The exponential decrease in irradiance is one of the major factors driving such patterns, as zooxanthellate corals are gradually replaced by low-light adapted macroalgae and exclusively-heterotrophic benthic taxa (Kahng et al. 2017). Consequently, this major shift in macrobiotic composition over depth results in decreasing similarity of the overall community with increasing vertical distance (between depths or depth ranges).

Although bathymetric trends of coral cover can vary greatly between region and individual locations, coral cover at upper mesophotic depths (30–60 m) in well-developed MCEs is often moderate or similar to shallower reefs (Glynn et al. 1996; Bak et al. 2005; Muir et al. 2015; Smith et al. 2016b, 2016c). Even at lower mesophotic depths (> 60 m), high coral cover can sometimes be observed, such as the *Leptoseris*-dominated communities at 70–90 m in Hawai‘i (Kahng and Maragos 2006; Pyle et al. 2016) and patches of *Agaricia*-dominated communities at 70–85 m depth in Curaçao (Hoeksema et al. 2016). However, these appear exceptions rather than the rule, with zooxanthellate coral cover generally decreasing with depth, and often only a few individual colonies observed towards the lower boundary of the mesophotic zone (Kahng and Maragos 2006; Englebert et al. 2014; Bongaerts et al. 2015b).

4.2 Community-level: change in scleractinian coral composition over depth

Scleractinian corals harboring photosynthetic endosymbionts occur from intertidal habitats down to depths in excess of 150 m (Maragos and Jokiel 1986; Veron 2000). No individual coral species covers this entire depth range, with the majority of species exhibiting distinct depth distributions (Goreau and Wells 1967; Sheppard 1982). Coral species have diversified to occupy distinct environmental niches along the depth gradient, exhibiting adaptations with regards to their morphology, physiology, and ecology (Done 1982). While distinct ecological assemblages can be observed across distinct reef habitats, many of the transitions in relation to the depth gradient are gradual and continuous rather than representing uniform boundaries (Kahng et al. 2017) or discrete communities with ecotones. Nonetheless, given this depth partitioning of individual species, the overlap in species composition decreases with increasing vertical distance (between depths or depth ranges).

The similarity between the scleractinian coral community at shallow and mesophotic depths is determined by the species with distributions that span both depth ranges. This can be considered either by determining presence/absence or by taking into account commonality (qualitative) or abundance (quantitative). When considering reported minimum and maximum depths for each species, a large proportion of all coral species would qualify as overlapping, with more than 75% of Caribbean scleractinian coral species occurring from the surface to ~30 m and almost half occurring down to ~50 m (Bridge et al. 2013). Similarly, based on presence/absence, more than 40% of *Acropora* species found on shallow reefs on the Great Barrier Reef have been reported at mesophotic depths (mostly 30–40 m) (Muir et al. 2015), and ~15–25% of the overall reef community (including fishes and other non-scleractinian taxa) were shared from shallow to lower mesophotic depths (60–150 m depth) (Semmler et al. 2017). When considering depth-generalist coral species that are considered common at both shallow and mesophotic depths (0–60 m), such overlap is likely much lower. For example, ~25% of Caribbean coral species (Bongaerts et al. 2010) and ~20% of *Acropora* species on the Great Barrier Reef (Muir et al. 2015) are considered common to both the shallow and upper mesophotic depths.

Furthermore, the overlap in species composition is based on traditional taxonomic species identification, which is heavily biased towards shallow-water diversity, particularly in the Indo-Pacific. Coral species that can occur over relatively large depth ranges (i.e., depth-

generalist species), often exhibit distinct phenotypes at opposite ends of their depth distribution, which is often attributed to phenotypic plasticity (Veron 2000; Lesser et al. 2010). Although, some of this phenotypic variation (e.g., in gross morphology or specific skeletal features) may instead reflect adaptive divergence and be associated with undescribed lineages or species (e.g., Bongaerts et al. 2011). In addition, phenotypic variation may go undetected (e.g., physiological rather than morphological differentiation) despite strong genetic divergence. Such cryptic diversity was discovered for the Caribbean species *Madracis pharensis* (Frade et al. 2010), with distinct lineages associated with shallow versus mesophotic depths (Bongaerts et al. 2015b).

4.3 Population-level: connectivity and reproduction over depth

Depth-associated differentiation represents a continuum of divergence, ranging from species-level divergence (as in the cryptic species example; Frade et al. 2010) to genetic differentiation at the population-level. This is relevant in terms of establishing the connection between distinct depth zones, and initial studies have demonstrated that a single depth-generalist species does not necessarily consist of a single panmictic population (Bongaerts et al. 2010, 2017; van Oppen et al. 2011; Brazeau et al. 2013; Serrano et al. 2014, 2016). Such genetic differentiation can be driven by physical dispersal barriers, such as local oceanographic features (Serrano et al. 2016) or ecological barriers, such as those associated with depth-related selection (Bongaerts et al. 2017). Genetic differentiation of populations does not necessarily occur at opposite depth extremes, but may occur between habitats with minimal difference in depth (e.g., front and back or flat and slope; Bongaerts et al. 2011; van Oppen et al. in review). Furthermore, despite the presence of gene flow, migration of individuals between distinct depth zones may be inferred to be strongly directional, occurring primarily down the slope or vice versa (Serrano et al. 2014). Connectivity can also be strongly affected by the reproductive success of corals at depth, with decreased fecundity and/or oocyte size reported for the majority of studied depth-generalist species (9 out of 11 species; Feldman et al. 2018; Prasetya et al. 2017; Shlesinger et al. 2018; Shlesinger and Loya 2018). An exception is *Orbicella faveolata* in the U.S. Virgin Islands, which was observed to exhibit increased fecundity at depth (Holstein et al. 2015). Thus, although species may have a distribution spanning multiple reef habitats or depth zones, migration and/or the extent of gene flow may be limited or non-existent (i.e., with distinct deep-water genotypes that do not

occur in the shallow), rendering the populations as separate units for purposes of conservation, or directional, resulting in source-sink relationships between distinct habitats.

With regards to connectivity between shallow (< 30 m) and mesophotic (≥ 30 m) populations, population genetic structure of six scleractinian species has been assessed: *S. hystrix* (van Oppen et al. 2011), *Montastraea cavernosa* (Brazeau et al. 2013; Serrano et al. 2014), *Porites astreoides* (Serrano et al. 2016), *Stephanocoenia intersepta* and *Agaricia fragilis* (Bongaerts et al. 2017), and *Agaricia lamarcki* (Hammerman et al. 2018). These assessments have demonstrated that coral species with similar ecological distributions can exhibit very distinct patterns of vertical connectivity (Bongaerts et al. 2017). At the same time, patterns of vertical connectivity within a single species can vary between regions, demonstrating the importance of location-specific extrinsic factors and regional oceanographic patterns (Holstein et al. 2016b; Serrano et al. 2016). The potential for vertical connectivity may be affected by species-specific life history traits, however, observed patterns remain ambiguous and further studies encompassing a broader range of species and locations are required to elucidate such relationships. Regardless, these initial assessments demonstrate that mesophotic to shallow migration may only be ecologically relevant (in terms of reseeded), for a subset of species shared between shallow and mesophotic depths.

4.4 Symbiont-level: associated microbiomes over depth

Scleractinian corals are known to associate with a consortium of endosymbionts, including eukaryotes and prokaryotes, many of which are expected to play an important role in the adaptation to specific reef environments (LaJeunesse 2002; Frade et al. 2008; Herndandez-Agreda et al. 2016). The endosymbiotic dinoflagellates of the genus *Symbiodinium* on which corals depend for photosynthesis represent a highly diverse group, with distinct physiological characteristics reflecting adaptation to different light and thermal conditions (Iglesias-Prieto et al. 2004; Sampayo et al. 2007; Frade et al. 2008). Single coral species have been demonstrated to associate with distinct *Symbiodinium* types over depth (Rowan and Knowlton 1995; Sampayo et al. 2007; Lucas et al. 2016), likely facilitating distribution across an environmental gradient (Frade et al. 2008). A survey in the southern Caribbean demonstrated that such symbiont zonation was a dominant feature among depth-generalist species, resulting in highly structured communities over depth and limited overlap between shallow and mesophotic communities, when considering coral host-*Symbiodinium*

associations together (Bongaerts et al. 2015a). Although endosymbiont association can be rather flexible for certain coral taxa (Serrano et al. 2016), other taxa appear to be more specific, with patterns of symbiont depth zonation reflected in underlying genetic divergence of the coral host (Bongaerts et al. 2010, 2011, 2017; Frade et al. 2010; Brazeau et al. 2013). Vertical transmission of depth-specialized symbionts (common in brooding corals) may potentially pose restraints on shallow-mesophotic connectivity (Bongaerts et al. 2010; but see Serrano et al. 2016). Depth-related patterns have also been observed for the prokaryotic communities associated with depth-generalist corals, with mesophotic corals harboring distinct prokaryotic taxa (Glasl et al. 2017; Hernandez-Agreda et al. 2017). Although our understanding of coral-prokaryote interactions at mesophotic depths is very limited (Olson and Kellogg 2010; Ainsworth et al. 2015), initial observations indicate that depth-specific microbial associations may be ubiquitous, further adding to patterns of holobiont differentiation over depth.

5. The role of depth refuges and refugia in overall reef persistence

Potential short-term refuges and long-term refugia at intermediate (15–30 m) or mesophotic depths (> 30 m) are important to the persistence of the communities themselves as their associated biodiversity and structural complexity is safeguarded. Given that the composition of coral reef communities over depth is governed by environmental gradients, these areas also share a certain extent of overlap in biodiversity with shallower communities. This overlap has led to the hypothesis that protected deeper reef communities may play an ecologically-important role in the persistence of populations, species, or potentially the broader coral reef community. The ability of deeper protected coral communities to act as a substantial, local source of recruitment (Hughes and Tanner 2010) is probably one of the most discussed functional roles (Holstein et al. 2015). The potential reseedling role was originally discussed as one of the premises of the DRRH (Bongaerts et al. 2010). Here, we consider this role separately from the ability to escape, resist, or recover through disturbances, and argue that in addition to (or in the absence of) reseedling potential, certain depth refuges could play an important functional role in facilitating local species persistence.

5.1 *Reseeding*: aiding in shallow reef recovery

We define *reseeding* as the substantial provisioning of viable propagules by safeguarded populations of (one or multiple) species at depth, aiding in the active recovery of disturbance-impacted shallower populations. The further specification of *mesophotic reseeded refuges* therefore corresponds largely to the DRRH as postulated in Bongaerts et al. (2010): deep reef areas that “(1) are protected or dampened from disturbances that affect shallow reef areas and (2) can provide a viable reproductive source for shallow reef areas following disturbance.”. When considering reef recovery, we classify reseeded as recruitment input substantial enough to reestablish populations within natural recovery timeframes (~5–15 years) (Connell 1997; Hughes et al. 2017). This requires either a substantial number of surviving individuals, or a highly-fecund population, with the ability to provide viable recruits to the shallows. The simplest example of a *reseeding refuge* would be that of a single species for which shallow representatives suffer complete mortality due to an episodic disturbance, with a substantial number of deeper representatives surviving and subsequently acting as a source of recruitment for shallow corals. Direct evidence of even such a simple species-specific reseeded refuge is still lacking, due to the current impossibility to track the fate of individual coral larvae and the difficulty of ruling out influx from less-disturbed, shallow populations in genetic studies. Nonetheless, there are definitely examples of panmixia over depth in species that are abundant at both shallow and mesophotic depths (Serrano et al. 2014, 2016; Bongaerts et al. 2017). While surviving populations in the mesophotic thermal refuge described for *S. hystrix* at Sesoko Island in Okinawa were found to be composed of lineages occurring elsewhere in the archipelago at shallow depths (Sinniger et al. 2017), recruitment into the shallow may be limited due to a reduced reproductive window at depth (Prasetia et al. 2017), and reestablishment of a shallow-water populations at this location (> 15 years later) has not yet been reported.

When evaluating reseeded refuges in the context of the entire coral community, the *disturbance/divergence trade-off* (Fig. 3) starts to play a major role in determining which species benefit (Bongaerts 2011; Bongaerts et al. 2017). Given a decreasing disturbance-impact over depth, the difference in impact on two considered depth ranges becomes greater the further they are apart (i.e., increasing depth-differential), with greater depths usually providing greater protection. However, with an increasing depth-differential, the two considered communities (at opposite depth ranges) also become more dissimilar, across all

taxonomic levels (Fig. 3). In terms of the scleractinian coral community, this basically means that the species pool of corals with potential to act as a source of recruitment becomes more limited with increasing depth. Although intuitively this would imply a greater reseed potential of shallow refuges, this is not necessarily the case as the disturbance/divergence trade-off is likely to be exacerbated at shallow depths given that changes in environmental factors and the impact of disturbances do not decrease linearly with depth. For example, while a disturbance may only affect reef flat habitat (0–2 m) and not the reef crest and slope (2–10 m), there may only be limited overlap in the community associated with these environmentally-distinct shallow-water habitats.

Given the disturbance/divergence trade-off, the potential for a multi-species mesophotic reseeded refuge is generally considered with respect to upper mesophotic (~30–60 m) rather than lower mesophotic (> 60 m) depths (Bongaerts et al. 2010; Kahng et al. 2014; Semmler et al. 2017). At lower mesophotic depths, the number of species shared with the shallow is expected to be very limited (but see Semmler et al. 2017), the probability for population-level differentiation higher, and the expected fecundity lower at such extreme depths (although empirical data in support of these expectations are still largely absent; but see Shlesinger et al. 2017; Shlesinger and Loya 2018). Initial qualitative assessments of the proportion of species on a reef that are common at both shallow and upper mesophotic depths report ~20–25% (Bongaerts et al. 2010; Muir et al. 2015), but such numbers are likely to vary across ranges (and are likely to change with more accurate quantitative assessments). Given that strong genetic differentiation is not uncommon across large depth ranges, and can hamper the exchange of recruits between depths, the mesophotic reseeded refuge concept applies to a subset of those shared species, and may therefore only be relevant to individual species rather than on the ecosystem-level (sensu Bongaerts et al. 2017).

The term *reseeded depth refugium* would apply to a repeated *reseeded refuge* scenario, where the depth refugium would actively aid in the (partial) recovery of a population or community after repeated or ongoing disturbances by acting as a source of recruitment. Given the difficulty of demonstrating depth refugia in general (as it requires assessment over multiple disturbances), demonstrating reseeded depth refugia is even more complicated because of the lack of direct evidence of deep to shallow reseeded. Currently the most parsimonious example of a (species-specific) reseeded depth refugium is the relatively shallow populations of *Millepora intricata* in the Eastern Tropical Pacific (Smith et al. 2014).

However, the evidence of this example is inferential and based on the apparent total extirpation of the shallow population (< 10 m) during the 1997-98 ENSO and then its reappearance after a few years hiatus, adjacent to surviving deeper populations (> 10 m). In addition, the ability to detect this process was due to unusual circumstances, involving a continuous coral reef ecological dataset, a restricted regional species range, and complete shallow water extirpation (Smith et al. 2014).

5.2 Local persistence: safeguarding biodiversity at depth

We define *local persistence* as the safeguarding of (one or multiple) species at depth, effectively negating local/regional species extinction, but with limited to no potential to aid in the recovery of shallow-water populations. The number of safeguarded individuals may be minimal and/or connectivity with a disturbed habitat may be limited or non-existent. Given that the depth-distributions of scleractinian corals (or the distribution of almost any species across an environmental gradient for that matter) are never continuous uniform and are characterized by distribution tails (when considering species abundance over depth), even predominantly shallow corals often have a small number of individuals occurring at greater depths. The number of such safeguarded individuals and their expected fitness (assuming their minimal abundance at that depth is reflecting suboptimal conditions) are lower, and so we propose that they are less likely to aid in the recovery of disturbed habitat through active reseedling (Holstein et al. 2015, 2016a). However, these safeguarded individuals have the potential to ensure the local persistence of the species, avoiding localized extinction (Bongaerts et al. 2013a; Muir et al. 2015), similar to the *mesophotic local persistence refuge* described for *S. hystrix* in Sinniger et al. (2017). Potentially, over longer timescales, they may even aid in the re-establishment of a substantial shallow population, although without the influx of long-distance migration, this could lead to a more susceptible population due to the associated genetic bottleneck. In this sense, the concepts of reseedling and local persistence are located on a continuum, from substantial to zero recruitment input into the shallow. Alternatively, a mesophotic local persistence refuge may safeguard individuals that are genetically distinct from those in the shallow (e.g., due to deep-water adaptation), and therefore, cannot successfully recruit to shallow depths. This could be particularly true for depth resilience areas, that may harbor genetically distinct individuals that are maladapted to shallow-water conditions. Despite this potential lack of connectivity, the taxonomic species may still be safeguarded in a geographic area through such a refuge, even though a certain

proportion of its genetic diversity (or one of its evolutionary significant units) may be eliminated.

Local persistence depth refuges may hold true for a large number of species albeit with a large variability in the number of individuals of each species that are safeguarded at depth. For example, during the 2016 bleaching event in the Maldives, the coral community at 24–30 m harbored representatives of almost 75% of the shallow-reef species assemblage, and experienced reduced bleaching effects (Muir et al. 2017). Although the number of safeguarded individuals may have been limited for many of these species (in comparison to their abundance at shallower depths), this depth refuge may have prevented local extinction for a reasonable proportion of shallow reef coral biodiversity. Conversely, species with very shallow distributions may therefore lack such local persistence depth refuges, and be more vulnerable to regional extinction (Smith et al. 2014; Muir et al. 2017). Again, species overlap decreases with increasing depth, but as persistence refuges are not necessarily dependent on depth-specific abundance and/or genetic differentiation, its potential remains considerably higher than compared to reseeded refuges. Consequently, mesophotic local persistence refuges may apply to a relatively large number of species.

In terms of *local persistence depth refugia*, the same attributes of local persistence at depth apply, although protection would need to be provided over multiple disturbances. Alternatively, although this timeframe exceeds the temporal scope considered in this review, when referring to local persistence depth refugia over geological timescales, it could refer to protection during long-term adverse conditions related to past climatic changes, and allowing for expansion when favorable conditions return at shallow depths. Regardless, unequivocally demonstrating the occurrence of such refugia face similar complications as reseeded depth refugia.

6. Conclusions

It is apparent that the concept of depth refuges/refugia can be considered in many shapes and forms, with the original DRRH encompassing only some of these (matching our description as a mesophotic reseeded refuge). Although we have attempted to provide initial structure by presenting these as delineated concepts, it is clear that all of these can be considered as part of a continuum. Most importantly, reviewing these concepts reiterates that the

refuge/refugium role of intermediate (15–30 m) and mesophotic (≥ 30 m) depths cannot be evaluated with a simple true or false answer.

There is evidence for depth refuges (including mesophotic refuges) from storms and thermal anomalies, indicating that these may have been ubiquitous in space and time. However, the exact impacts over depths are case-specific and there are many intricacies to consider when evaluating impacts beyond just a single taxon. There is little evidence to support that areas that have provided depth refuge scale to refugia. In fact, the increasing frequency and severity of both storm and bleaching events, and accumulating reports of impacts reaching mesophotic depths, cast doubt on the ability of depth refuges to provide protection over the long-term (over multiple disturbances). Nonetheless, there is a critical lack of longitudinal studies at mesophotic depths, hampering the evaluation of their role as refugia. We also stress the importance of looking beyond avoidance, and consider the potential of differential resilience at depth. Resilience at depth could be conveyed through increased resistance or recovery rates at particular locations, but remains an aspect that is poorly explored. Looking more holistically at refuges as areas buffered, but not necessarily removed, from disturbance and the potential for resilience to maintain mesophotic reefs through resistance and recovery has led to the idea of mesophotic oases, or areas where interacting suites of these processes favor persistence in a changing ocean.

In terms of the functional role of depth refuges/refugia, the described disturbance/divergence trade-off predicts that such contributions decrease with an increasing depth differential. We argue that the role as reseeding refuges likely represents a taxon-specific concept that does not likely scale up across a broad range of species, given that it only applies to depth-generalist species and of those, only to the subset of depth-generalist species that freely exchange recruits across depth. In contrast, local persistence refuges, may be applicable across a broad range of coral species, potentially representing an underappreciated functional role of depth refuges. Particularly when it comes to function, the disturbance/divergence trade-off highlights that it may be beneficial to evaluate depth refuges without the bias of the arbitrarily defined upper limit of mesophotic coral ecosystems, given that the most functionally valuable refuges may arguably be located at intermediate-mesophotic depths (e.g., 20–40 m).

Evidence regarding these concepts remains largely circumstantial, and while depth refuges may be likely and could buy time in the face of an increasingly inimical climate, they will not

protect biodiversity long-term if they do not scale up to refugia. In outlining this conceptual framework and reviewing the relevant empirical data, we hope to provide a foundation for further discussion and research into the different aspects of depth refuges and refugia.

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962 **Figures**

964 **Figure 1.** Conceptual scenarios of coral cover/richness trajectories at depth. In the diagram
965 disturbance is increasing through time, reflecting a system under increasing thermal stress
966 and/or storm impacts.

Figure 2. Different qualifiers to characterize persistence at depth.

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971 **Figure 3.** Conceptual diagram illustrating the “disturbance/divergence trade-off.” With
 972 increasing depth, the impact of disturbances generally decreases, however, at the same time,
 973 the community also becomes more divergent (from the shallow). Therefore, the optimum in
 974 terms of the functional value of a *depth refuge* is likely to be situated at intermediate/upper-
 975 mesophotic depths (e.g., ~20–40 m). Adapted with permission from Bongaerts (2011).